Models of Animals in Their Home Range

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Abstract. In this work we provide a flexible stochastic model for the movement of territorial mammals in their home range, that is, a model with as few parameters as possible, that exhibits the type of territorial dynamics that has been observed in the field. Our final objective is to develop an experimental model useful for the study of biological processes from the perspective of resource management.

Key words. Animal movement models, home range, mark-recapture probabilities, abundance studies, resource management, stochastic models.

1. INTRODUCTION.

An animal's home range consists of the area or volume over which an animal normally travels in pursuit of its routine activities (Burt, 1943). The study of animal movement has been limited to the delineation of the home range (Mohr, 1947; Hayne, 1949; Dice and Clark, 1953; Calhoun and Casby, 1958; Brown, 1962; Sanderson, 1966; Jewell, 1966; Jennrich and Turner, 1969; Mazurkiewicz, 1969, 1971; Koeppl et al., 1975, 1977; Dunn and Gipson, 1977; Cooper, 1978; Ford and Krumme, 1979, Macdonald et al., 1980; Voigt and Timme, 1980; Schoener, 1981; Anderson, 1982; Samuel et al., 1985). The need to develop models that incorporate the characteristic movement of individuals within their home range has not been carried out systematically despite the fact that its study is essential for the development of effective management and ecological studies. Models that mimic the movement of individuals within their home range can help in the development of statistical models for the estimation of trap-dependent capture and recapture probabilities for animals with multiple nuclei of activity . These estimates are necessary for estimating the abundance of these populations. Movement models can aslo help in the estimation of encounter rates between potential mating individuals. A better understanding of mating and better estimates of abundance are central to the management of wildlife as well as to the field of behavioral ecology. In summary, detailed models of animal movement that describe realistic behavioral patterns may not only be important to management, wildlife studies, and behavioral ecology but they may also be useful for the refinement and testing of statistical approaches for the assessment of biological diversity.

Mobility is an important aspect in the life history of many organisms. The movement and/or dispersal of organisms can be visualized at the level of the individual, perhaps the result of responses to localized information or, at the level of the group, which may be the result viable evolutionary strategies. The first may impact the local distribution patterns while the second may impact the global distribution patterns, for example, insect locomotion is divided by Southwood (1962) into two behavioral categories: migration and trivial movement. Kareiva (1981) divides insect locomotion into migratory and non-migratory movement. Migratory movement corresponds to attempts of leaving one's habitat while non-migratory movements deal with short-range movement that has played an important role in the structuring of insect-plant interactions (van Emden, 1972; Mound and Waloff, 1978; Price, 1980). As Kareiva (1981) points out
". movement while foraging and egg-laying determines rates of insect-plant encounter, such

movements implicitly underlie phenomena such as associational resistance...locomotory ambits are profoundly sensitive to the structure of the local plant community...". Elton (1949) remarks on the observed clumping in animal communities and pushes for the incorporation of the effects of patchy environments in mathematical models. MacArthur and Wilson's (1967) theory of island biography provided the first significant theoretical advance in this program (see also Levin, 1978a, b). Most of these theoretical studies are concerned with the evolutionary mechanisms and/or strategies that maintain the observed ecological and genetical diversity. The modeling of the movement of individual organisms under different assumptions helps understand its role on the structure and dynamics of a population in different environments.

Animal movement has been studied using different approaches instigated, perhaps, by Pearson's remark on the stochastic nature of animal paths (see Pearson, 1905, 1906). Kareiva and Shigesada (1983) classify movement models into two categories: general diffusion models (Skellam, 1951, 1973; Broadbent and Kendall, 1953; Patlak, 1953a, b; Scotter et al., 1970; Okubo, 1980; Turchin, 1989, 1991) and simulation models (Siniff and Jenssen, 1969; Kaiser, 1976; Jones, 1977, Zalucki and Kitching, 1982). Diffusion models have been useful to model approximate limiting distributions of the movement of organisms and have benefited from a highly developed mathematical theory (see Levin, 1986; Levin and Castillo-Chavez, 1989). As Okubo (1980) points out, these models are valid when the observation time is much longer than the duration of the average individual step and when the spatial scale of observation is substantially greater than the length of each animal's step. Research on diffusion models has been quite extensive, and applications have been found not only to the movement and dispersal of organisms but also to the spread of genotype frequencies (Fisher, 1937; Aronson and Weinberger, 1975), the spread of epidemics (see for example Kendall, 1965; Diekmann, 1978, 1979; Thieme, 1977; Hadeler, 1984), and to the asymptotic speed of advance in plant dispersal, invasion, and disease dynamics (Skellam, 1951; Okubo, 1986; F. van den Bosch, 1990; Lubina and Levin, 1988). Simulation models may produce accurate descriptions of movement processes, but comparisons are exceptionally difficult (Marsh and Jones, 1988). The theoretical work in this area is quite extensive and we only highlight a few important models that are relevant to the approach that we follow.

Kareiva and Shigesada (1983) developed a correlated random walk model which represents a viable compromise between diffusion and simulation models—a compromise between realism and generality. They develop a procedure that quantifies movement sequences in terms of step size and turning angle probability distributions. Their formulae allow for the comparison of different searching behaviors and their consequences. Other authors follow their approach (Kareiva and Odonell, 1987; McCulloch and Cain, 1989; Cain, 1991) but never in the context of studying animal movement in a home range.

Sniff and Jessen (1969) simulated the movement of individual red foxes within their home range using radio-telemetry data. Sniff and Jessen matched the observed speed movement distribution to a gamma distribution, and the observed relative angle distribution to a circular normal distribution. Although their model produced realistic descriptions of movement processes, it was not possible to use it in a biological context, for example, in the differentiation of animals' patterns (pattern recognition).

Holgate (1971) developed biased random walk models and encourage their use in the problem of estimating the probability that an animal is caught in its home range. Holgate constructed stochastic models using two different movement mechanisms based on the attraction of animals

to a center of activity. The stochastic processes used by Holgate were built in a squared lattice. The first model assumes attraction to a pre-specified center of activity, a nest which contains offspring waiting to be fed, and, consequently, the probability of taking a step in the direction of the nest is greater as the animal moves farther away from it (see also Kac, 1947). The second model assumes that attraction to the home center depends solely on the animal's memory and familiarity--mechanisms that are harder to define mathematically (see also Gilles, 1956). It is assumed that attraction to the center of activity diminishes hyperbolically with distance, that is, the farther away an animal is from its home the less likely it is to return. Therefore, the mean traveled distance from the center of activity does not, in general, converge to a limit and, consequently, animals are more likely to disperse (Okubo, 1980). Intuitively, however, the difference between the mechanisms suggested by Holgate appears clear: the memory-familiarity process is overtaken by diffusive tendencies and, in principle, may lead to an unbounded home range; alternatively, if the attraction to the nest increases with distance, then the diffusive tendencies associated with this random walk model may be overshadow by the attraction, at appropriately large distances, leading to bounded home ranges. The use of Holgate's stochastic models with a pre-specified center of attraction makes it possible to construct animals' paths that are realistic (see, Bovet and Benhamou, 1988). Unfortunately, in Holgate's models after an animal reaches its center of activity, it remains there forever. Because Holgate's models can be reduced to the study of difference equations for the transition probabilities, if smaller and smaller steps are taken then, on the limit, it converges to a generalized diffusion equation which it may possible to analyze (see Batschelet , 1971; Okubo 1980). We use a modified and expanded version of Holgate's second approach to construct the model in this article.

Dunn and Gipson (1977) and Dunn and Brisbin (1985) suggested the use of the Orstein-Uhlenbeck Diffusion Process (multivariate centrally biased diffusion process) to approximate the "true movement of an animal" in its home range. The animal' paths are generated by a continuous, stationary Gaussian Markov process for which the probability of movement depends on the distance to the animal's center of activity and to the position of animal "close" neighbors. However, for many animals, the Orstein-Uhlenbeck Diffusion Process does not provide a realistic model for movement (see Worton, 1987). More recently, Benhamou (1989) developed a model, for the movement of mammals within their home range, based on a first order correlated random walk model that integrates a differential klinokinetic mechanism (see also Bovet and Benhamou, 1988). Benhamou's model assumes that an animal moves in a radial olfactory gradient field centered around its center of activity, with the intensity of the associated olfactory stimulus decreasing with distance. The model requires that the animal moves at random each time it reaches home (the center of activity), a situation that occurs frequently. That is, there is a single nuclei of activity which is visited often.

Field studies of different mammal species show the existence of multiple areas of high activity in an animal's home range (see reviews by Voigt and Tinline, 1980; Don and Reynolds, 1983); hence, the useof a unique center of activity in the modeling of an individual's home range is too limiting. Don and Reynolds (1985) support the theoretical and practical need of modeling animal movemeent in a multinuclear home range, that is, in a home range with multiple centers of activity. These researchers introduce, as a partial solution, a parametric method for estimating the forms of the animal's utilization distribution in a multinuclear home range. However, they do not provide specific models for the movement of animals in multinuclear environments.

Bell (1991) focusses on the importance of incorporating changes in locomotory patterns over time in simulation models of an animal's path. Bell concentrates on the role of active versus non-

active periods. An animal begins its active period movement searching for food, water, or other resource. A random walk model thus provides a reasonable first approximation for the early stages of the active period. As time elapses, the tendency to return home—or, more generally, to a nucleus of activity—increases. Hence, realistic models of animal movement in their home range need to incorporate time since departure from the center of activity. Our model integrates these effects introducing few additional parameters.

In the next section, we describe a model that incorporates in a crude manner several of the features observed in field studies, including multiple nuclei and time since departure from a nucleus. Our objective is to develop a flexible model, that is, a model with as few parameters as possible, that exhibits the type of territorial dynamics observed in the field. We plan to use this model as a tool for developing, testing, and evaluating resource management strategies.

2. A MODEL FOR THE MOVEMENT OF ANIMALS IN THEIR HOME RANGE.

In this manuscript, we introduce a simple stochastic simulation model that reproduces the movements of animals in multinuclear home ranges. It is based on a random walk model that takes into account the time since departure from one of the nuclei or one of the centers of activity. Each nucleus has its own "stochastic basin" of attraction. Our main objective is to develop a flexible construct that mimics field territorial dynamics with a minimal number of parameters.

2a. Model with one nucleus (center) of activity.

Attraction towards a center of activity will be a function of time since departure from it. Animals begin the day wandering at random, or more explicitly, an individual moves in a lattice with eight possible future distinct adjacent locations. An individual remains at its current location or moves to an adjacent location. The time-dependent stochastic process records the position of an individual at time t from its center of activity, where t denotes the time since departure. To describe ξ_t explicitly, we assume the existence of finitely many adjacent sites (eight in our case). If S denotes the set of all sites in a two-dimensional (integer) lattice centered at the animal's center of activity, then ξ_t is a function defined on S with values in $R^+ \cup \{0\} = (0,\infty)$. At $t = 0$, the animal is at the center of activity. and as the time t changes, the animal either moves or stays, that is, jumps or does not jump to an adjacent (one of eight) point in the lattice.

The dynamics (the trajectory of an animal) is described by the time-dependent transition (or flip) rates at which the individual moves, that is, by the non-autonomous rates at which the animal jumps from location to location (individuals are allowed to stay put). These rates are given by a set of nonnegative numbers $\{c(x,y): x \neq y\}$. Each $c(x,y)$ denotes the rate at which the system changes from position x to position y (only eight distinct adjacent positions are available at any point in time), that is,

$$P(\xi_{t+h} = y \mid \xi_t = x) = c(x,y)h + o(h), \text{ for all } t \geq 0.$$

Explicitly,

$$P(\xi_{t+h} = y_i \mid \xi_t = x) = \lambda e^{-(\alpha d_i)}h + o(h), \text{ for all } t \geq 0$$

where α is the coefficient of attraction; y_i the coordinates of one of the eight points adjacent to point x in the lattice (positions are relative to the center of attraction); and d_i denotes the distance from y_i to the center of attraction (here the origin). The size of each square in the lattice is determined by the average distance traveled by an individual per unit time.

2b. Simulation of the process {t:t0}.

From the construction of the transition rates we know that

$$c(x) = \sum_{y \in S} c(x,y) < \infty.$$

We let the sequence $0 = \sigma_0 < \sigma_1 < \sigma_2 < \cdots$ denote the times at which the animal moves (jumps). Then $\tau_n = \sigma_n - \sigma_{n-1}$ has an exponential distribution with rate $c\left(\xi_{\sigma_{n-1}}\right)$, and we can simulate the process using the following procedure:

(i) Set the initial state ξ_0 by placing the individual at the center of activity, that is, $\xi_0 = 0$, and assume that a sequence of n jump times $0 = \sigma_0 < \sigma_1 < \cdots < \sigma_n$ and their corresponding states or positions ξ_{σ_i}, $1 \le i \le n$ have been determined.

(ii) Get τ_{n+1} from $\exp\left\{c\left(\xi_{\sigma_n}\right)\right\}$ and let $\sigma_{n+1} = \sigma_n + \tau_n$.

(iii) Set $\xi_{\sigma_{n+1}} = y_i$ with probability $\dfrac{c\left(\xi_{\sigma_n}, y_i\right)}{c\left(\xi_{\sigma_n}\right)}$.

(iv) Define $\xi_t = \xi_{\sigma_n} = x$ for $\sigma_n \le t \le \sigma_{n+1}$.

At the end of each day, we reset the clock to $t = 0$.

2c. Model with at least two nuclei of activity.

A simple modification of the above model allows for the incorporation of multiple areas of high activity, nuclei, or homes. Each nucleus has an associated coefficient of attraction that weights the effect of the nucleus on the animal's decisions. The effect depends on the distance to the nucleus and the time since departure. At time $t = 0$, the animal begins its movement from a particular center of attraction. Motion is initially random. As time progresses, however, motion itself does with some probability bring the individual animal within the "stochastic basin" of attraction of a different center of activity. Such attraction becomes stronger as time since departure progresses and, consequently, an animal tends to spend a proportion of its life in different centers of activity.

The modified transition rates are as follows:

$$P\left(\xi_{t+h} = y_i \mid \xi_t = x\right) = \lambda e^{-(\alpha_k t D_{ik})} h + o(h), \text{ for all } t \ge 0$$

where α_k is the coefficient of attraction of nucleus k; y_i the coordinates of one of the eight points adjacent to point x in the lattice (y_i is measured relative to the origin, which is assumed to be the main center of attraction c_0); D_{ik} denotes the distance from y_i to c_k, the (k+1) center of attraction. The size of each square in the lattice is determined by the average distance traveled by

an individual per unit time. The simulation follows exactly the same procedure as before, except that the number of transition rates has now increased.

3. SPACE USE PATTERN GENERATED BY THE MODEL

We ran our model with one center of activity to estimate the space use pattern for one realization. Each realization corresponds to a activity period (e.g., one night in nocturnal animals). We also vary grid size and α to see the effect of these changes in the space use patterns. We let the realization run for 7000 steps in a 100x100-cell grid, where each cell is 100 units per side, and also with a 200x200-cell grid, where each cell is 50 units per side; we let α vary between 0.00001 and 0.0000001. Figure 1 (α=0.00001, 100x100 grid) represents a space use pattern very concentrated around the center of activity. Figure 2 (α=0.000001, 100x100 grid) represents more sparse activity with the highest activity level in the center. Figure 3 represents sparse activity with no preference for the center (α=0.0000001, 100x100 grid). Figure 4. (α=0.000001, 200x200 grid), which shows the effect of reducing the grid, essentially conveys the same picture as Figure 2, but with added detail. Therefore, while α determines space use patterns, pattern details depend on cell size. If we have an animal with highly concentrated activity close to a nucleus, it will be important to work with small cell sizes.

The utilization distribution is defined by Van Winkle (1975) as "the two dimension relative frequency distribution for the points of location of an animal over a period of time." Van Winkle found that a bivariate normal distribution adequately characterizes the home range of many animals. Each of the previous simulations can be interpreted as a random sample (of size one) from a utilization distribution. An empirical sample distribution is obtained by running 100 realization with α=0.000001, a 100x100-cell grid, and a cell size of 100 units per side (Figure 5). This figure looks roughly like a bivariate normal distribution with its center at the nucleus of activity.

We ran the multinuclear model with three centers of activity for 7000 steps in a 100x100 grid (cells of 100 units per side). We estimated 30 realizations to obtain a utilization distribution with each of the three coefficients of attraction α_i set at 0.000001Figure 6. As shown in Figure 6, there are three peaks in the utility distribution, all with similar sparse distributions. In Figure 7, we also observe three peaks, but with varying degrees of attraction. In this case, we set α=0.00001 for a single nucleus—the one that shows the concentrated activity. The other two nuclei remained at 0.000001.

4. DISCUSSION

We develop a model that represents animal movements in a home range. It is general enough to allow comparisons between animals using the parameter α, thus improving on detailed simulation models. It has only one parameter (α) which is related to the size of the home range. Therefore, α summarizes how powerful is the need to look for resources and how strong is the attraction to the center of activity. Since home range increases with animal body size (MacNab, 1963; Armstrong, 1965; Schoener, 1968; Turner et al., 1969; Harestad and Bunnell, 1979; Peters, 1983), it may be expected that α will also vary as a function of body size. A further complication that we have not addressed deals with the problem of generating accurate estimates of home range size (see Macdonald et al., 1980; Dunn and Brisbin, 1985). Knowledge of home range size

is implicitly assumed in our simulations, and α must be calibrated to take into account the size of the home range.

As discussed earlier, Dunn and Gipson (1977) and Dunn and Brisbin (1985) proposed the Orstein-Uhlenbeck Diffusion Process to describe, in a very limited way, animals' movements in their home range (Worton 1987). Our model represents path averages because it only takes into account whether or not the animal is in a particular lattice square. Hence, such average behavior depends on the size of the cells in the lattice. This dependence disappears when a continuos model is used. So a diffusion approximation to our model could improve our model and it may make it amenable to mathematical analysis at least in a few special cases.

Although our model works on a lattice using a random walk, as Holgate's (1971) did, it presents some advantages over Holgate's approach, as the probability of movement not only depend on distance from the center of activity, but also on time since departure. The animal returns to its home without the use of reflecting boundaries. Our model allows the animal to move when it is at the center of activity, and implements the concept of multinuclear home range introduced by Don and Reynolds (1983).

Benhamou (1989) developed a model which represents mammals movements within its home range with a single center of activity. Animals move in a radial olfactory gradient field centered at the nucleus of activity—the intensity of olfactory stimulus decreasing with distance. A similar interpretation can be given to α in our model. Benhamou assumed a linear relationship between distance and intensity. Because in our model the dependence with distance is exponential, animals are very likely to return when they are far from home. Furthermore, since the probability of return is time-dependent, a function of the time since departure, the attraction to the center increases as the end of the animal's active period approaches. However, because both effects are weak at the beginning of the activity period, in such early stages we also observe a random walk. These two temporal/spatial effects combine to generate, if α is chosen appropriately, realistic utilization distributions without having to reposition the animal at the center of activity when the distance to its home is shorter than a step's length. Moreover, movement does not have to be forced-started with a random walk, as Benhamou's model requires. The animal arrives to its home range when its searching activities are finished and stops there to rest.

A common assumption in some of the mark-recapture methods used to estimate the density of animal populations is that each animal has a constant and equal probability of capture on each trapping occasion (Otis et al. 1978). More general models assume unequal and time-varying capture probabilities or behaviorally dependent capture probabilities, including trap shy or trap happy variants (see Otis et al., 1978; Pollock et al., 1990). However, no model assumes variation in capture probabilities as a function of the distribution of encounter between animals and traps in a multinuclear home range. Our model may help develop improved methods for the estimation of these probabilities. Specifically, our model may help develop methods that improve our current estimates of the probability of capture, by traps, of an animal in its home range. If the investigator possesses detailed spatial information of home ranges of particular species, he/she may be able to use our model to estimate the probability distribution of being capture by a trap as a function of where the trap is located within the home range. and, finally, be able to improve current estimates of abundance.

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REFERENCES

Anderson, D.J. (1982). The home range: A new nonparametric estimation technique. Ecology, 63:103-112.

Armstrong, J.T. (1965). Breeding home range in the nighthawk and other birds: Its evolutionary and ecological significance. Ecology, 46:619-629.

Batschelet, E. (1971). Record of preplanned and spontaneous discussion. Random Walk models for animal behaviour. In: G.P. Patil, E.C. Pielou, and E.W. Waters (eds.), Statistical Ecology, 2. Sampling and Modelling Biological Population and Populations and Population Dynamics, pp. 9-10. Pennsylvania State University Press.

Bell, W. (1991). Searching Behaviour: The Behaviour Ecology of Finding Resources. Chapman and Hall., NY.

Benhamou, S. (1989). An olfactory orientation model for mammals' movements in their home ranges. J. Theor. Biol., 139:379-388.

Bovet, P., and S. Benhamou (1988). Spatial analysis of animals' movements using a correlated random walk. J. Theor. Biol., 131:419-433.

Broadbent, S.R., and D.G. Kendall (1953). The random walk of Trichostrongylus retortaeformis. Biometrics, 9:460-466.

Brown, L.E. (1962). Home range in small mammal communities. In: B. Class (ed.), Survey of Biological Progress, Vol. 4, pp. 131-179. Academic Press, NY.

Burt, W.H. (1943). Territoriality and home range concepts as applied to mammals. J. Mamm., 24:346-352.

Cain, M. (1991). When do treatment differences in movement behaviours produce observable differences in long-term displacements? Ecology, 72(6):2137-2142.

Calhoun, J.B., and J.U. Casby (1958). Calculation of home range and density of small mammals. U.S. Public Health Monogr., 55:iv,1-24.

Cooper, W.E. (1978). Home range criteria based on temporal stability of areal occupation. J. Theoretical Biology., 73:687-695.

Dice, L.R., and P.J. Clark (1953). The statistical concept of home range as applied to the recapture radius of the deermouse (Peromyscus). Contrib. Lab. Vert. Biol., Univ. Michigan, 62:1-15.

Diekmann, O. (1978). Threshold and traveling waves for the geographical spread of infection. Journal of Mathematical Biology, 6:109-130.

Diekmann, O. (1979). Run for your life: A note on the asymptotic speed of propagation of an epidemic. Journal of Differential Equations, 33:58-73.

Don, B.A.C., and K. Reynolds (1983). A home range model incorporating biological attraction points. J. Anim. Ecology, 52:69-71.

Dunn, J.E., and P. Gipson (1977). Analysis of radio telemetry data in studies of home range. Biometrics, 33:85-101.

Ford, R.G., and D.W. Krumme (1979). The analysis of space use patterns. J. Theor. Biol., 76:125-155.

Gillis, J. (1956). Centrally biased discrete random walk. Quart. J. Math (2), 7:144-152.

Hadeler, K.P. (1984). Spread and age structure epidemic models. In: Perspectives in Mathematics, Anniversary of Oberwolfach, pp. 295-320. Birkhauser-Veralg, Basel.

Harestad, A.S., and F.L. Bunnell (1979). Home range and body weight: A reevaluation. Ecology, 60:389-402.

Hayne D.W. (1949). Calculation of size of home range. J.Mamm., 30:1-18.

Holgate (1971). Random Walk models for animal behaviour. In: G.P. Patil, E.C. Pielou, and E. W. Waters (eds.), Statistical Ecology, 2. Sampling and Modelling Biological Population and Populations and Population Dynamics, pp. 1-9. Pennsylvania State University.

Jennrich, R.I., and F.B. Turner (1969). Measurement of non-circular home range. J. Theoret. Biol., 22:227-237.

Jewell, P.A. (1966). The concept of home range in mammals. In: P.A. Jewell and C. Loizos (eds.), Play, Exploration and Territory in Mammals, pp. 85-109 (Symp. Zool. Soc. London, 1966, No. 18). Academic Press, NY.

Jones, R.E. (1977). Movement patterns and egg distributions in cabbage butterflies. Journal of Animal Ecology, 46:195-212.

Kaiser, H. (1976). Quantitative description and simulation of stochastic behaviour in dragonflies (Aeschna cyana, Odonata). Acta Biotheor., 25:163-210.

Kareiva, P.M. (1981). Non-migratory movement and the distribution of herbivorous insects: Experiments with plant spacing and the application of diffusion models to mar-recapture data. Ph.D. dissertation. Cornell University, Ithaca, NY.

Kareiva, P.M., and N. Shigesada (1983). Analyzing insect movement as a correlated random walk. Oecologia (Berlin), 56:234-238.

Kareiva, P.M., and G.M. Odonell (1987). Swarms of predators exhibit "preytaxis" if individual predators use area-restricted search. American Naturalist, 130:233-270.

Koeppl, J.W., N.A. Slade, K.S. Harris, and R.S. Hoffmann.(1977). A three dimensional home range model. J. Mamm., 58:213-220.

Koeppl, J.W., N.A. Slade, and R.S. Hoffmann.(1975). A bivariate home range model with possible application to ethological data analysis. J. Mamm., 56:81-90.

Levin, S.A. (1978a). Population models and community structure in heterogeneous environments. In: S.A. Levin (ed.), Populations and Communities, pp. 439-476. Studies in Mathematical Biology, Vol II, Mathematical Association of America, Washington, DC

Levin, S.A. (1978b). Pattern formation in ecological communities. In: J.H. Steele (ed.), Spatial Pattern ij Plankton Communities, pp. 433-465. Plenum Press, NY

Levin, S.A. (1986). Random walk models of movement and their implications. In: T.G. Hallam and S.A. Levin (eds.), Mathematical Ecology. Biomathematics Vol. 17. Springer-Verlag, Berlin.

Levin, S.A., and C. Castillo-Chavez (1990). Topics in Evolutionary Biology. In: S. Lessard (ed.), Mathematical and Statistical Developments of Evolutionary Theory, pp. 327-358. NATO ASI Series, Kluwer Academic Publishers, London.

Lubina, J.A., and S.A. Levin (1988). The spread of a reinvading species: Range expansion in the California Sea Otter. Am. Nat., 131:526-543.

MacArthur, R.H., and E.O. Wilson (1967). The Theory of Island Biography. Princeton University Press, Princeton, NJ.

Macdonald, D.W., F.G. Ball, and N.G. Hough (1980). The evaluating of home range size and configuration using radio tracking data. In: C.J. Amlaner and D.W. Macdonald, A Handbook on Biotelemetry and Radio Tracking, pp 405-424. Pergamon Press.

MacNab, B.K. (1963). Bionergetics and the determination of home range size. American Naturalist, 97:133-140.

Marsh, L.M., and R.E. Jones (1988). The form and consequences of random walk movement models. J. Theor. Biol., 133:113-131.

Mazurkiewicz, M. (1969). Elliptical modification of the home range pattern. Bull. Acad. Polonaise Sci., 17:427-431.

Mazurkiewicz, M. (1971). Shape, size and distribution of home ranges of Clethrionomys glacereolus (Schreber, 1780) Acat Theriol., 16:23-60.

McCulloch, C.E., and M.L. Cain (1989). Analysing discrete movement data as a correlated random walk. Ecology, 70:383-388.

Mohr, C.O. (1947). Table of equivalent populations of North America small mammals. Am. Midl. Nat., 37:223-249.

Mound, L.A., and Waloff, N. (1978). Diversity of insect faunas. Symp. Roy. Ent. Soc. Lond., 9. Blackwell, London.

Okubo, A. (1980). Diffusion and Ecological Problems: Mathematical Models. Springer-Verlag, NY.

Okubo, A. (1986). Dynamical aspects of animal grouping: Swarms, schools, flocks, and herds. Ad. Biophys., 22:194.

Otis, L.D., K.P. Burnham, G.C. White, and D.R. Anderson (1978). Statistical inferences from capture data on closed populations. Wildlife Monographs, 62.

Patlak, C.S. (1953a). Random walk with persistence and external bias. Bulletin on Mathematical Biophysics, 15:311-358.

Patlak, C.S. (1953b). A mathematical contribution to the study of orientation of organisms. Bulletin on Mathematical Biophysics, 15:431-476.

Pearson, K. (1905). The problem of the random walk. Nature, 72:294.

Pearson, K. (1906). A mathematical theory of random migration. Mathematical Contributions to the Theory of Evolution, XV. Draper's Company Research Memories, Biometrics Series, III, s.

Peters, R.H. (1983). The Implications of Body Size. Cambridge University Press, Cambridge.

Pollock, K.H., J.D. Nichols, C. Brownie, and J. Hines (1990). Statistical inferences for capture-recapture experiments. Wildlife Monographs, 107.

Price, P.W. (1980). The Evolutionary Biology of Parasites. Princeton University Press, Princeton, NJ.

Samuel, M.D., D.J. Pierce, and E.O. Garton (1985). Identifying areas of concentration use within home range. J. Anim. Ecol., 54:711-721.

Sanderson, G.C. (1966). The study of mammal movements: A review. J. Wildlife Management, 30:215-235.

Schoener, T.W. (1981). An empirical based estimate of home range. Theor. Popul. Biol., 20:281-325.

Schoener, T.W. (1968). Sizes of feeding territories among birds. Ecology, 49:123-141.

Scotter, D.R., K.P. Lamp, and E. Hassan (1970). A dispersal parameter. Ecology, 52:174-180.

Siniff, D.B., and C.R. Jenssen (1969). A simulation model of animal movement patterns. Advances in Ecological Research, 6:185-219.

Skellam, J.G. (1951). Random dispersal in theoretical population. Biometrika, 38:196-218.

Skellam, J.G. (1973). The formulation and interpretation of mathematical and diffusionary models in population biology. In: M.S. Bartlet and R.W. Hiorns (eds.), The Mathematical Theory of Dynamics of Biological Populations, pp 63-85. Academic Press.

Southwood, T.R.E. (1962). Migration of terrestrial arthropods in relation to habitat. Biol. Rev., 37:171-214.

Thieme, H. (1977). A model for the spread of an epidemic. Journal of Mathematical Biology, 4:337-351.

Turchin, P. (1989). Beyond simple diffusion: Models of not-so-simple movement in animals and cells. Comments in Theoretical Biology, 1:65-83.

Turchin, P. (1991). Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. Ecology, 72(4):1253-1266.

Turner, F.B., R.I. Jennrich, and J.D. Weintraub (1969). Home range and body size lizards. Ecology, 50:1076-1081.

van den Bosch, F. (1990). The velocity of spatial population expansion. Ph.D. dissertation. State University of Leiden.

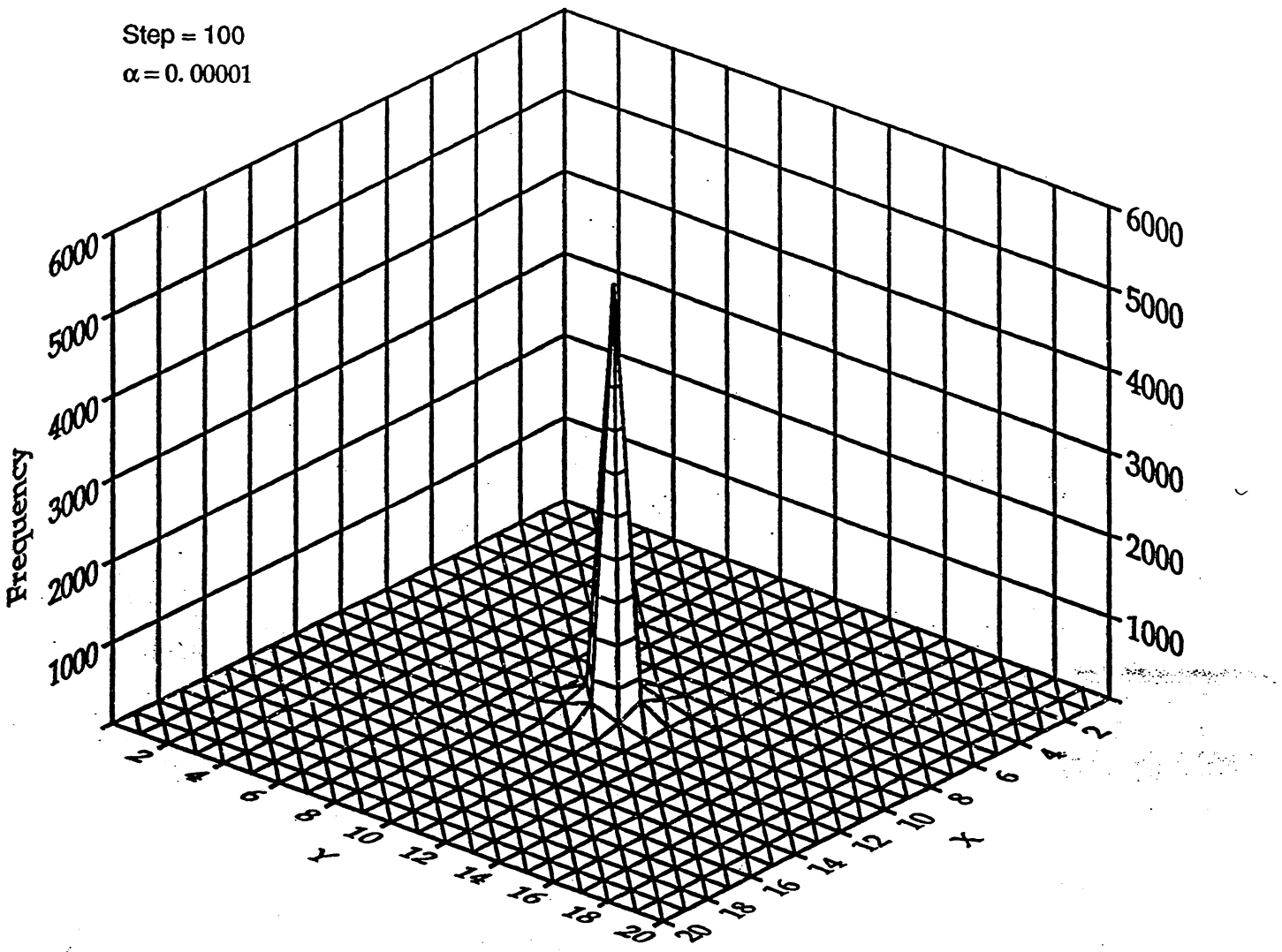
van Emden, H.F. (1972). Insect/plant relationships. Symp. Roy. Ent. Soc. Lond., 6. Blackwell, London.

Van Winkle, W. (1975). Comparison of several probabilistic home-range models. J. Wild. Manage., 39:118-123.

Voigt, D.R., and R.R.Tinline (1980). Strategies for analyzing radio tracking data. In: C.J. Amlaner and D.W. Macdonald, A Handbook on Biotelemetry and Radio Tracking, pp 387-404. Pergamon Press.

Worton, B.J. (1987). A review of models of home range for animal movements. Ecological Modeling, 38:277-298.

Zalucki, M.P., and R.L. Kitching (1982). Component analysis and modelling of the movement process: The simulation of simple tracks. Res. Popul. Ecol., 24:239-249.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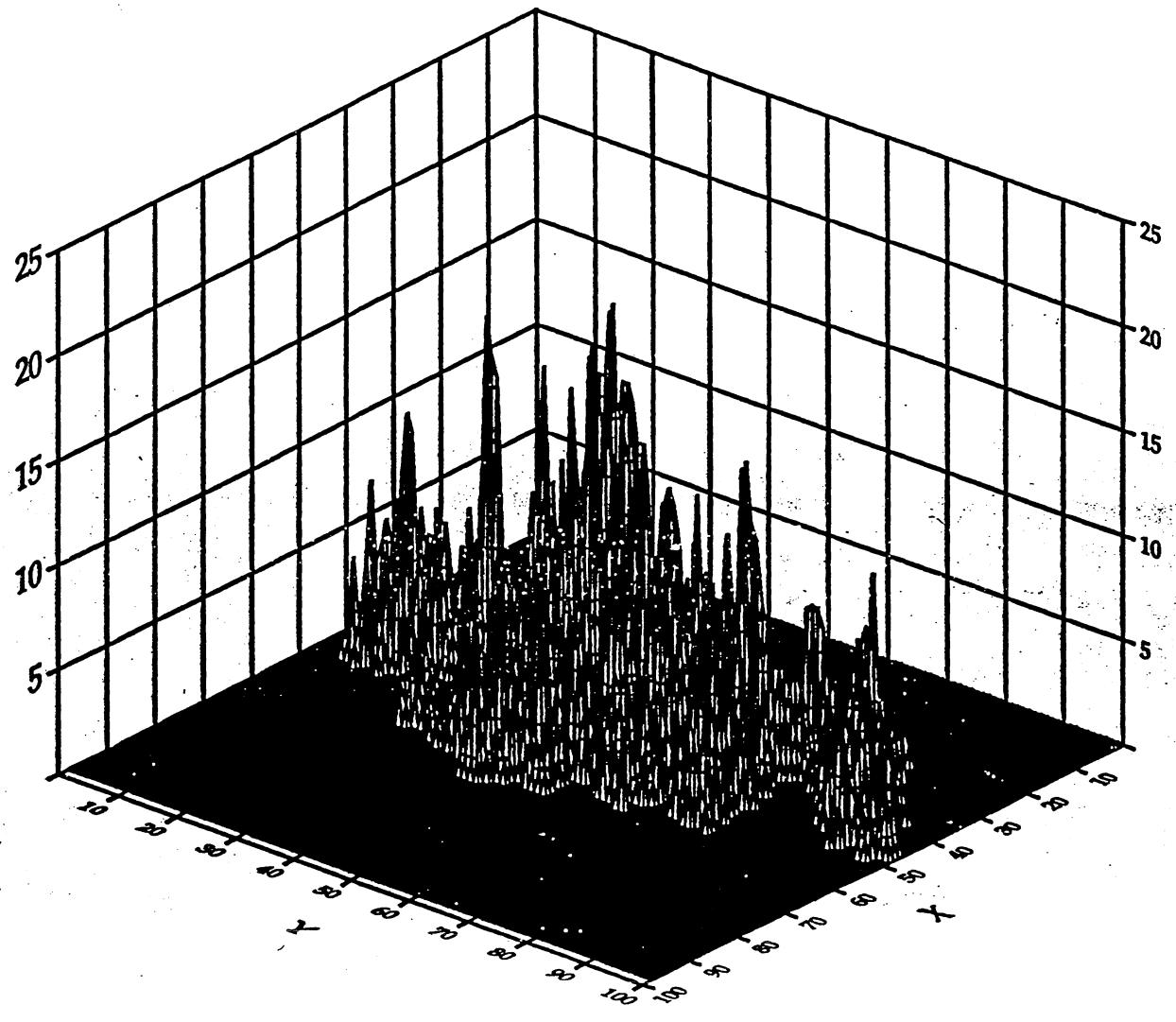

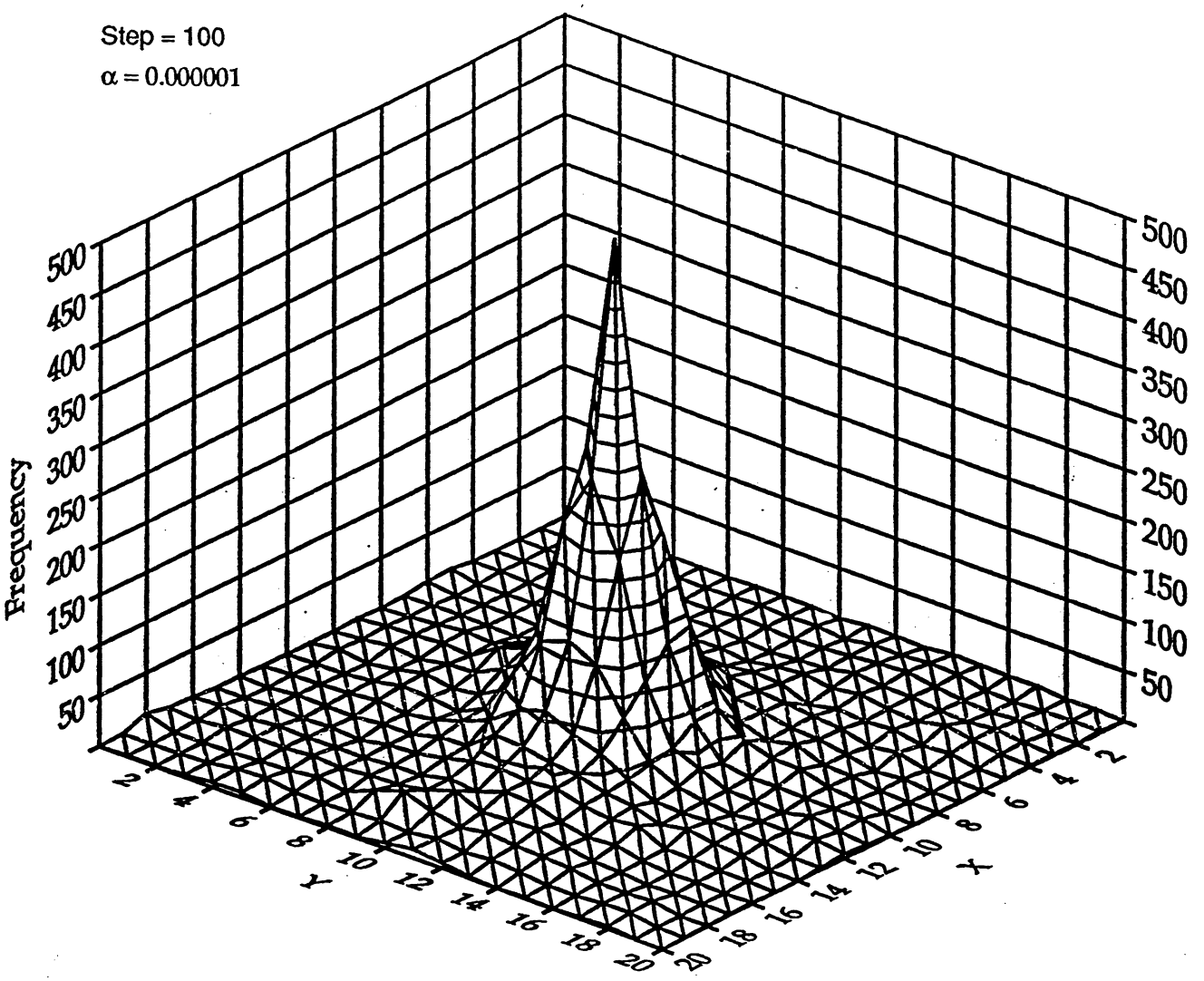
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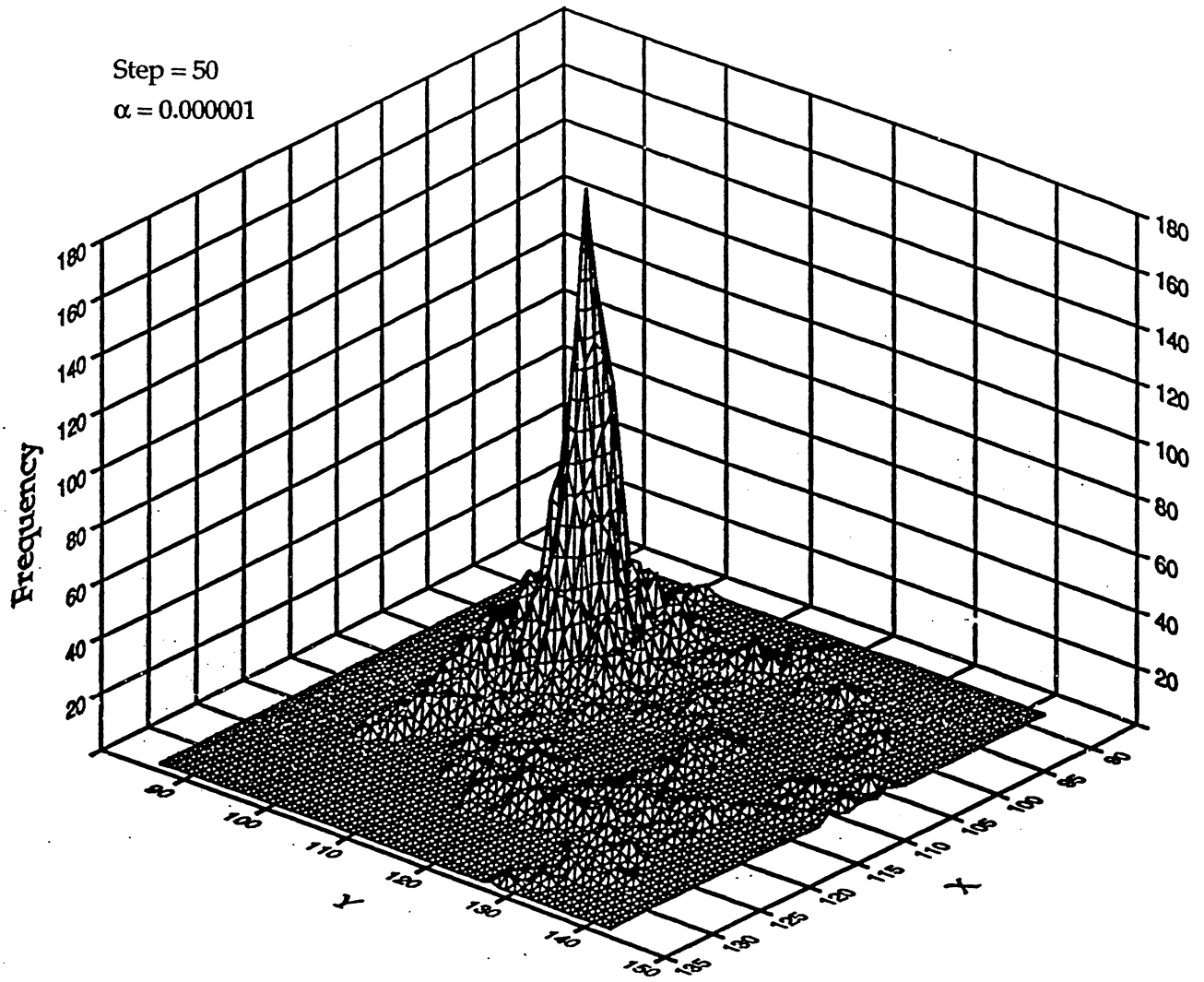
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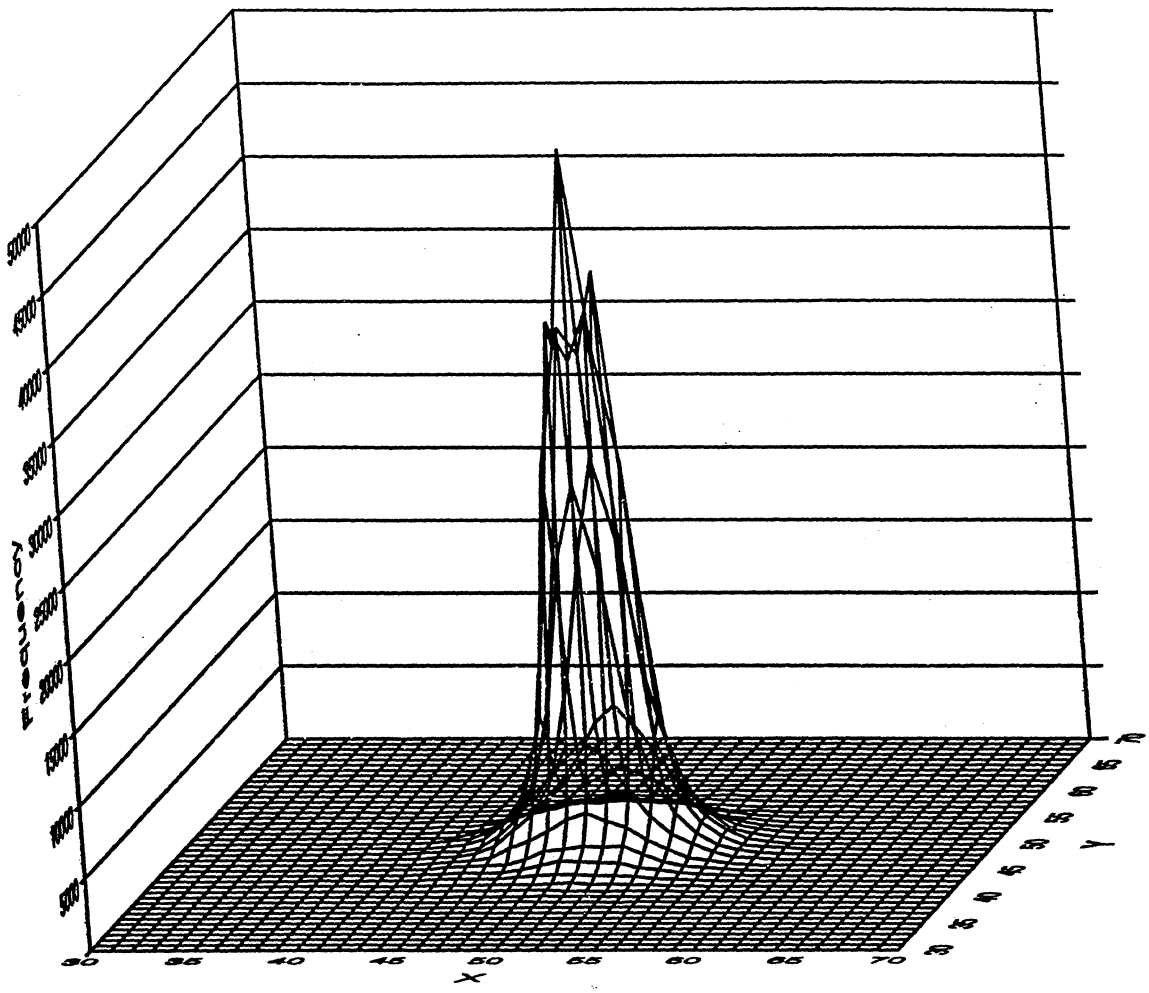
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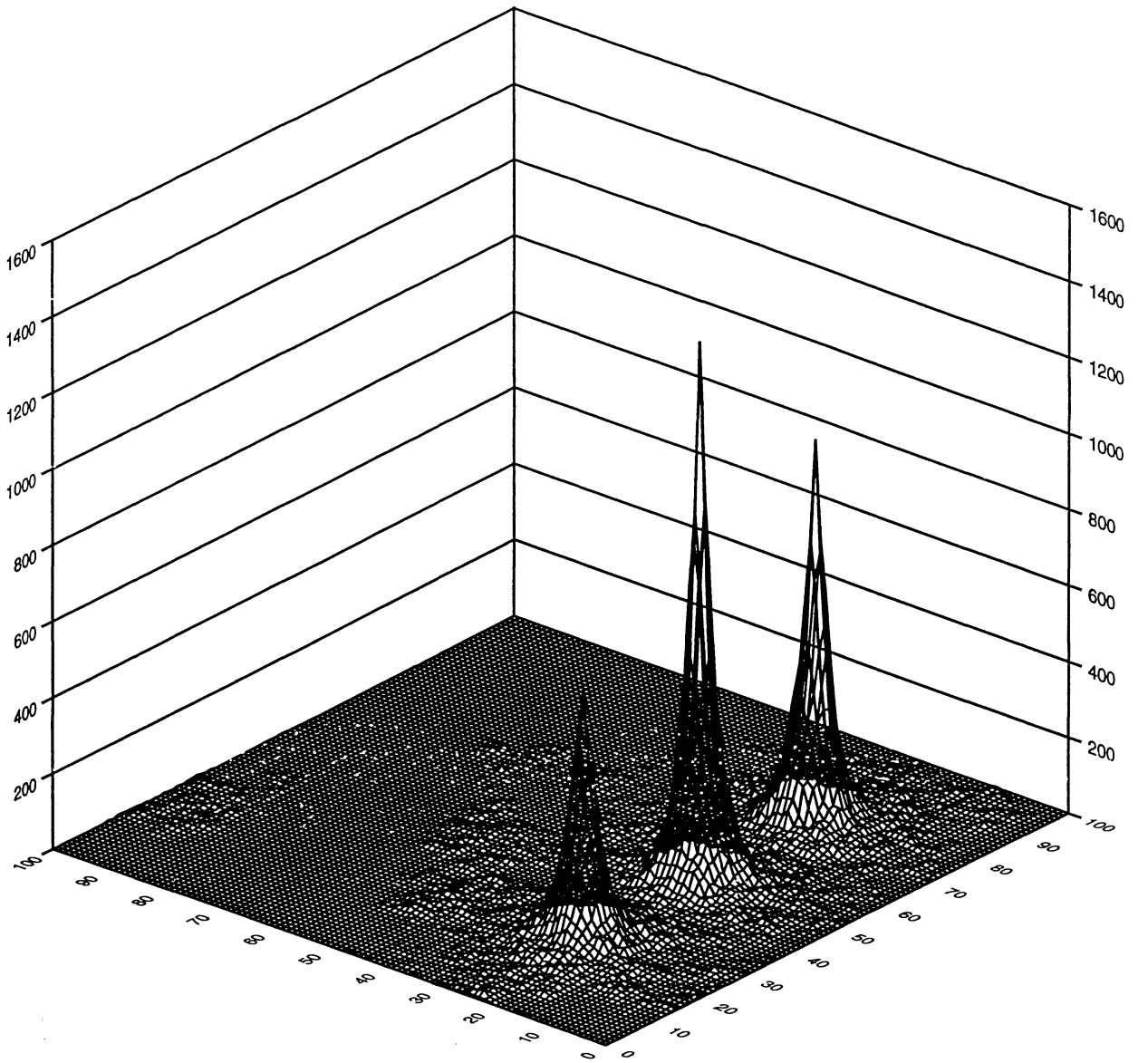
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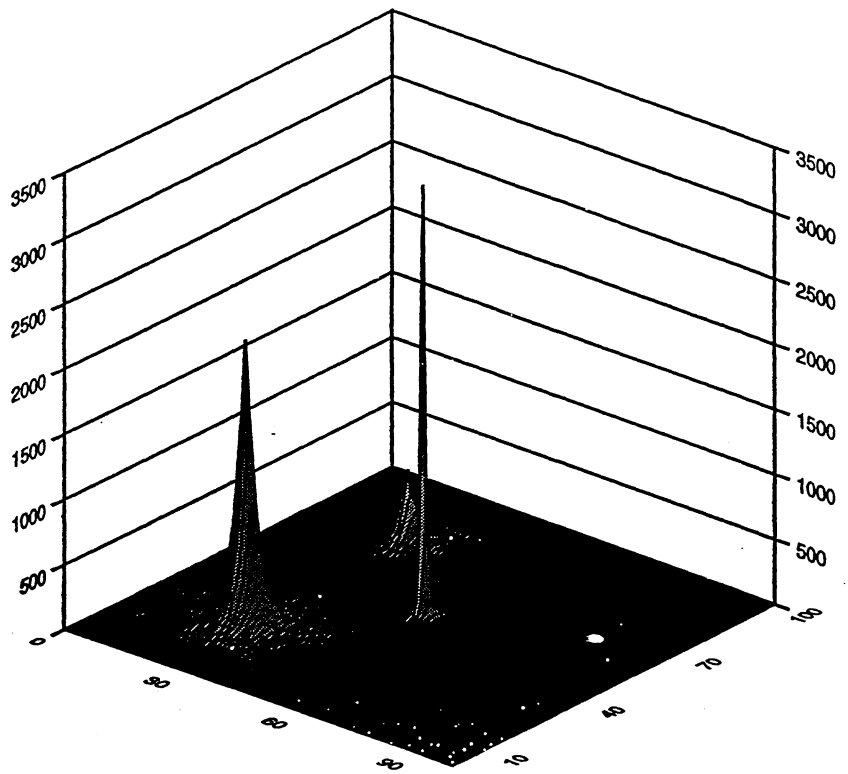
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